5.—The Physiology of Sclerophyll Plants

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The physiology of sclerophylls growing in areas of Mediterranean type climate throughout the world is reviewed. Particularly in so far as their water economy is concerned there is evidence that such sclerophylls differ markedly from the xerophytes and mesophytes of the type studied by Maximov at Tiflis. The available data on the origin and function of xeromorphic characters in sclerophylls is also examined and the need for further research to clarify the position here is stressed.

Introduction

The publication of "Die Pflanzenwelt von West Australien" by Diels in 1906 following his visit in 1901-1902 forms one of the major landmarks in the botanical history of Western Australia. Diels, trained at a time when Schimper's "Plant Geography upon a Physiological Basis" (1898, 1903) was profoundly influencing botanical thought, not only gave due weight to the floristic side (as expressed in "Fragmenta Phytographiae Australiae occidentalis" (1905) which he published jointly with Pritzel) but also laid the foundations of plant geography and ecology. Within the framework of his introductory account of the elements of the vegetation of the whole continent, the picture of the vegetation of South Western Australia stands out in clear relief. It is to Diels that we owe, among other things, the delimitation of the South Western and Eremean botanical provinces, the characterisation of the overall vegetation formation, the first coherent account of the plants which determined the physiognomy of the vegetation, and a basic discussion of the growth forms and of the peculiarities of leaf morphology and structure of South Western and marginal Eremean vegetation types.

Using the nomenclature of the time, Diels characterised most of the hard-leaved evergreen vegetation as being xerophytic. The leaves were observed to be modified in a variety of ways from the usual conception of a normal soft mesomorphic leaf characteristic of plants growing in temperate regions of the northern hemisphere. These modifications together with the pale dull-green or grey appearance of many of the leaves gave, he considered, a distinctive look to Australian vegetation. This same feature is characteristic of course of hard-leaved evergreen vegetation throughout the world, whether it be the South West part of the Cape region of South Africa, the Mediterranean countries, California or Central Chile. The term *sclerophyll*, coined by Schimper (1903) applies very aptly to this kind of vegetation. Diels described and classified the various kinds of sclerophylls in the West Australian area under the headings of Moderate Sized Sclerophyll leaves, Ericoid leaves and Needle-like leaves. He also emphasized the importance of the condition of aphylly in the Western Australian sclerophyll vegetation pointing out many instances where winged stems took over the functions of the leaf. Adamson and Osborne (1924) described and classified the sclerophylls of South Australia. They used the term Broad Leaf Sclerophyll while retaining the Ericoid and Needle-leaf types. Patton (1932) described similar sclerophyll leaf types in Victoria. The various morphological and structural modifications characteristic of Australian sclerophylls are set out in Table I. By virtue of possessing these modifications they are described as being *xeromorphic*. This descriptive term is used because such characters are commonly present in vegetation which grows in dry localities and distinguishes it from the vegetation of moister more temperate areas which lack them. The possession of xeromorphic modifications is not, of course, peculiar to sclerophylls. The Australian tomentose succulents for example, also show xeromorphic characters and together with sclerophylls they are referred to as *xeromorphs*.

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TABLE I

Morphological and Structural Modifications Characteristic of Australian Sclerophylls

Illustrated with Examples from Western Australia

Broad and leathery leaves
> *Stirlingia latifolia*
> *Conospermum scaposum*
> *Banksia grandis*
> *Eucalyptus marginata*
> *Acacia cyanophylla* (phyllode)

Microphylly—the Ericoid leaf
> *Micromyrtus imbricata*
> *Astroloma macrocalyx*
> *Bossiaea eriocarpa*
> *Hibbertia hypericoides*

Acicular or Needle Leaf
> *Grevillea acerosa*
> *Hakea recurva*
> *Hovea pungens*

Aphylly
> *Hibbertia conspicua*
> *Bossiaea leptacantha*
> *Daviesia aphylla*

Winged stems
> *Acacia alata*
> *Sphaerolobium alatum*
> *Trachymene compressa*

Spiny stems
> *Cryptandra parvifolia*
> *Psammomoya ephedroides*

Sunken stomata
> *Hakea clavata*
> *Acacia acuminata*
> *Daviesia pachyphylla*

Cutinization and lignification
> *Eucalyptus* spp.
> *Hakea* spp.
> *Daviesia* spp.

Development of tannins and resinous substances
> *Hakea varia*
> *Acacia acuminata*
> *Dodonaea viscosa*

Strong development of palisade mesophyll and weak development of spongy mesophyll
> *Eucalyptus marginata*

Presence of hairs and scales or waxy bloom on surface
> *Lachnostachys verbascifolia*
> *Eucalyptus caesia*

Interest has long centred around the question as to whether the xeromorphic modifications of sclerophylls (and of other plants in arid or semi-arid areas) have physiological significance for survival and distribution. This paper reviews the available data on peculiarities of physiology in sclerophylls with special reference to Australian vegetation, and endeavours to ascertain to what extent they are related to the characters of morphology and structure associated with the sclerophyll habit. The structural features were early held to affect the water relations of sclerophylls and much study has been devoted to this point. The first section therefore deals with their water relations. This is followed by an examination of their assimilation, respiration and general metabolism, leading on to a discussion of theories of the significance and origin of the sclerophyll habit and xeromorphic characters.

The Water Relations of Sclerophylls

Transpiration

Probably the most typical and certainly the most highly developed sclerophyll vegetation in the world occurs in parts of Australia, and the study of its physiology has engaged the attention of several botanists. Using a potometer method Wood (1923) in South Australia studied the transpiration of *Eremophila scoparia*, *Geijera parviflora* and *Casuarina lepidophloia* during summer in a 9.2 inch rainfall area at Dilkera, 90 miles north of Adelaide. He observed (see Table II) that the rates of water loss were not high in *Eremophila* or *Geijera* and that they did not respond readily to changes in environmental conditions. In *Casuarina* the rate was definitely higher and more subject to fluctuations in evaporating power of the air. Wood concluded that the higher rate of transpiration in *Casuarina* during the day and its correspondence to the curve for evaporation was due to the ability of high winds, common in the area, to sweep along the line of stomates in the furrows of the branchlets. For *Eremophila* and *Geijera* the reduction in transpiration was ascribed to their xeromorphic modifications and the presence of vapours from oily secretions. Working in a somewhat more arid area at Curnamona (250 miles north-east of Adelaide) with a rainfall of only 7.0 inches, Wood (1924) obtained additional information on the transpiration rates of sclerophylls and of a mesomorph (*Senecio magnificus*) (see Table II). The rate of water loss from the mesomorph which was growing where water was available, was much greater than that of the three sclerophylls listed. Of the three sclerophylls, the less thickly cutinised *Acacia victoriae*, which grows in water courses and swampy areas, transpired more rapidly than *Acacia aneura* and *Eremophila glabra* with their more pronounced structural modifications.

Additional results (see Table II) were obtained by Wood (1934) at Koonamore (8.4 in. rainfall) and in the Mount Lofty Ranges (20-40 in. rainfall). It may be noted that the rates of transpiration in the Mount Lofty experiments are much higher than those recorded in summer for sclerophyll plants growing in the more arid

areas at Dilkera, Curnamona and Koonamore, although the rate of evaporation is lower in the ranges. This higher transpiration rate may be referable to more abundant soil moisture at the time (not reported) when these experiments were performed.

In this paper Wood (1934) used the concept of *Relative Transpiration* so that he could compare his results with those of other workers. He concerned himself more with the mean relative transpiration of the group rather than with that of individual plants and came to the conclusion that sclerophyll plants in South Australia and high moor plants in Germany (Firbas, 1931) showed no significant difference in transpiration when the relative transpirations were compared by the difference of their means.

At Melbourne in Victoria, Wilson (1924) studied the rates of water loss (using a weighing method) from intact seedling sclerophyll plants growing in pots. The aim of this work was to determine whether such plants could modify water loss, particularly during hot north wind days. He concluded that provided the available water supply was adequate, the plants had no special powers of accommodation, the rates of transpiration being quite high over long periods (see Table II). Wilson's results indicate a very high rate of water loss for sclerophylls under the conditions of his experiments. In this connection it may be noted that Henrici (1937) in South Africa, found that potted xerophytic plants could display a very high transpiration rate, but in plants tested in the field the rate was much lower. Wilson's results therefore can not be considered as being typical for field conditions in summer. The author (1946-1947) carried out experiments on sclerophylls in various parts of Victoria; Mallee country, heathland near Melbourne, Mt. Macedon and the Bogong High Plains. Results (Table II) consistently showed much lower rates of transpiration for all the sclerophylls tested than those recorded by Wilson.

Experiments on transpiration of Western Australian sclerophylls in the Perth area in late summer have also been carried out by the author during the period 1949 to 1953. Typical results obtained are shown in Table II. Restriction of transpiration occurred in sclerophylls as the dry season advanced. A mesomorph growing in the area (*Erechthites hispidula*) showed a considerably higher rate of water loss before it eventually wilted permanently and died.

Many investigations on the transpiration of sclerophylls have been made in other parts of the world, notably in the Mediterranean area, in South Africa and in California. A summary of the results of this work recalculated where necessary in mg./sq. dm./min. or mg./g./min. is presented in Table III.

Guttenberg (1907) using a weighing potometer method studied the transpiration of sclerophylls on the island of Lussin off the Yugoslav Adriatic coast. He reported then that in summer transpiration was not greatly reduced although later (1927) he modified his view. Study of his 1907 results shows that a considerable reduction in rate does in fact occur on passing from the spring to the summer and also that (particularly when his results are recalculated in terms of the area of both sides of the leaf in certain cases) the rates are relatively low in summer.

Cooper (1922) working in California made preliminary observations on the rate of water loss in broad sclerophyll (Chaparral) during summer (Table III). While the results given are limited it may be noted that the values are relatively low.

Oppenheimer (1932) investigated the water economy of sclerophylls in the Palestine area (Table III) and showed that there was a marked restriction of transpiration during the hot and dry summer months, this restriction being associated with a state of more or less pronounced physiological rest.

Rouschal (1938) made a thorough study of the water relations of Maquis sclerophyll vegetation of Rovigno on the north eastern Adriatic coast.

He placed Maquis plants in three categories in so far as transpiration was concerned: those with low transpiration rate under all conditions, those which limit their transpiration with increasing dryness (a large group), and those with high transpiration under favourable conditions. From a study of his data it appears that transpiration, though high under favourable conditions showed reduction in all cases as the dry season advanced (Table III). Results in several cases were comparable to those of Guttenberg and Oppenheimer.

Montemartini (1930) in Italy also worked with representative Maquis plants and his results for *Ceratonia* and *Nerium* indicated that Maquis sclerophylls in general showed a parallelism between their transpiration rate and physiological activity.

Killian (1932) investigated the rates of transpiration in Algerian Maquis and found that in typical sclerophylls transpiration during the dry season was low and regular while in mesmorphic plants it was considerably higher.

Henrici (1940) at Pretoria in South Africa, compared the rates of water loss from sclerophylls and mesomorphs growing in the same area. She found that the average rate of loss in sclerophylls was relatively low while that in associated mesomorphs was much higher (Table III).

Poljokoff (1946) in Palestine closely examined the water economy of the sclerophylls *Ceratonia* and *Olea* and showed that transpiration was relatively low and regular throughout the dry season. By contrast the loss of water from a mesomorphic plant (almond) growing in the area was strikingly high (Table III).

Eckardt (1952) studied the transpiration of Garrigue vegetation (a modified form of sclerophyll) in the Narbonnaise (Mediterranean) region. All the species he worked with showed considerable reduction of transpiration during the dry period.

The work on transpiration in the central and eastern Mediterranean areas was reviewed by Oppenheimer (1951) who pointed out that the average transpiration in summer for the Maquis type of vegetation seldom rose above 5 mg./g./min., while that of mesomorphs growing in these areas was strikingly higher.

TABLE II

Rate of Transpiration in Sclerophylls in Australia

Name of Investigator.	Location.	Date of Experiment	Method	Test Plants	Average Rate ‡ mg./ sq.dm./ min.	Maximum Rate mg./ sq.dm./ min.	Average Rate mg./ g./mm.
Wood* (1923)	Dilkera, Sth. Aust. (9·2 in. rainfall)	May (near end of five month's drought period)	Potometer ...	Eremophila scoparia	1·15	1·67 (2–3 p.m.)	..
				Geijera parviflora	0·36	0·55 (2–3 p.m.)	..
				Casuarina lepidophloia	2·25	4·45 (2–3 p.m.)	...
				Atmometer	111·1	....	....
Wood* (1924)	Curnamona Sth. Aust. (7·08 in. rainfall)	Summer ...	Potometer	Eremophila glabra	0·85	1·46 (2–3 p.m.)	..
				Acacia aneura	1·38	2·23 (2–3 p.m.)	...
				Acacia victoriae	4·75	8·86 (2–3 p.m.)	....
				Senecio magnificus (mesomorph)	15·70	23·0	.
				Atmometer	223·0	....	
Wood* (1934)	Koonamore Sth. Aust. (8·4 in. rainfall)	.... ..	Potometer	Casuarina lepidophloia	1·50	....	
				Geijera parviflora	0·32	....	..
				Eremophila scoparia	0·94	....	...
				Atmometer	75·0 †	....	...
				Eremophila glabra	1·03	....	...
				Acacia aneura	0·91	....	....
				Acacia victoriae	2·68	....	...
				Atmometer	108·0 †	....	
Wood* (1934)	Mount Lofty Ranges, Sth. Aust. (20–40 in. rainfall)	....	Weighing of cut shoots	Eucalyptus leucoxylon	26·60	....	...
				Acacia pycnantha	25·40	....	..
				Hakea rugosa	21·80	....	....
				Leptospermum myrsinoides ..	7·00	....	....
				Calythrix tetragona	8·65	....	....
				Hibbertia stricta....	12·18	....	...
				Atmometer	87·1	....	.
Wilson* (1924)	Melbourne, Victoria (25·5 in. rainfall)	February (late summer)	Interval weighing of intact seedlings in pots	Banksia serrata	58·3	....	..
				Eugenia smithii	21·8	....	..
				Atmometer (free water surface)	180·7	....	..
				Casuarina luehmanni	40·3	....	..
				Acacia pycnantha . .	17·5	....	..
				Eucalyptus macrorrhyncha ..	15·2	....	..
Grieve (hitherto unpublished data)	Walpeup, Victoria (Mallee) (10–12 inches rainfall)	September, 1946	Potometer ..	Eucalyptus dumosa . .	5·5	10·0	...
				Eremophila glabra	3·3	3·6	....
				Acacia ligulata	1·8	2·0	..
				Heterodendron oleifolium (herbaceous xerophyte)	1·3	2·7	..
				Atmometer	86·0	118·0	..
Do. do	Bogong High Plains, Victoria	January, 1947 (Summer)	Potometer	Eucalyptus gigantea	4·1	....	....
				Acacia falciformis	4·0	....	....
				Atmometer	86·1	....	....
Do. do.	Mt. Macedon, Victoria	February, 1947	Potometer	Eucalyptus gigantea	6·3	12·7	....
				Acacia melanoxylon (gully plant)	2·0	....	...
				Atmometer	78·0	....	
Do. do.	Oakleigh-Frankston, Victoria, (Sandheath). (25·5 in. rainfall)	February, 1947	Rapid weighing	Banksia collina	4·0	....	....
				Leptospermum laevigatum	1·1	....	....
				Hibbertia sericea	3·5	....	....
				Platylobium obtusangulum	2·2	....	....
				Atmometer (Filter paper "leaf")	25·0	....	....
Do. do.	Perth area, Western Australia, (32–34 in. rainfall)	1950 (late summer)	Rapid weighing	Hibbertia hypericoides	....	....	2·2
				Bossiaea eriocarpa	....	....	0·3
				Casuarina fraseriana	....	....	2·9
				Conostephium pendulum	....	....	2·8
				Eucalyptus calophylla	7·8	....	4·2
				Hardenbergia comptoniana	1·2	....	1·3
				Stirlingia latifolia	5·8	....	2·3
				Banksia attenuata	8·3	....	4·2
				Erechthites hispidula (mesomorph)	15·8	....	13·3
				Atmometer (Filter paper "leaf")	42·0	....	31·4

* Values recalculated to mg./sq.dm./min. (1923, 11 a.m.–6 p.m.), (1924, 8 a.m.–4 p.m.).   † Actual values in Wood's paper x 10.

‡ Transpiration rate is given in mg./sq.dm./min. for the total area of test leaves (*cf.* Rouschal, 1938).

Examination of the results in Table III shows that this holds true also for the sclerophylls of the western end of the Mediterranean and for those of South Africa and California. For typical sclerophylls in Western Australia under summer conditions, the author has found average rates to be below 5 mg./g./min. Results have also been calculated as mg./sq. dm./min. to facilitate comparison with earlier work in Victoria and it would appear that results obtained by the author for sclerophylls there, are generally below the equivalent of 5 mg./g./min. Wood's results (1923, 1924, 1934) using the potometer method show an average rate below the equivalent of 5 mg./g./min. The transpiration results for sclerophylls of the Mt. Lofty area using the weighed shoot method are, however, well above Oppenheimer's average figure. These may, as indicated earlier, have shown a high transpiration rate because of favourable soil moisture conditions which would obtain if the experiments were done in late spring or early summer. In the Perth area the author has found that rates of transpiration of sclerophylls are high during the transition period into summer but decline markedly later. Wilson's high results for well watered seedling sclerophylls growing in pots are not considered to be typical of water loss for natural growing vegetation. It is held that the author's more recent work under field conditions gives a clearer indication of the transpiration pattern for Victoria.

Summarizing the above it is appears that many sclerophylls in southern Australia when studied under field conditions during the dry summer period have, as compared with mesomorphs growing in the same areas, a relatively low average rate of transpiration. The same is true of sclerophylls in other parts of the world. The question as to whether this restriction of transpiration is related to the xeromorphic modifications of sclerophylls described earlier or to other aspects of their physiology, will be returned to in a later section.

TABLE III

Rate of Transpiration in Sclerophylls of the Mediterranean Area, U.S.A. and South Africa

Name of Investigator	Location	Method	Test Plant	Average Rate* mg./sq.dm./min. Favourable Conditions	Average Rate* mg./sq.dm./min. Dry Conditions	Average Rate* mg./g./min. Dry Conditions	Maximum Rate Dry Conditions
Guttenberg (1907)	Is. of Lussin, Northern Jugoslavia, Adriatic Coast (Maquis)	Weighing Potometer	Laurus nobilis Arbutus unedo Olea europaea Ceratonia siliqua Pistacia lentiscus	2·66 8·50 3·66 3·00 2·50	1·66 2·91 3·75 .. 2·16	....	
Cooper (1922)	California (Chaparral)	Weighing Potometer	Adenostoma Arctostaphylos Arbutus	....	1·0–1·8 0·66–1·1 0·5	....	..
Oppenheimer (1932)	Palestine (Maquis)	Rapid weighing	Ceratonia siliqua Arbutus andrachne Laurus nobilis Prunus amygdalus (mesomorph)	....	... .	0·17 0·22 0·37 15·8	
Rouschal (1938)	Rovigno, N.E. Adriatic Coast (Maquis)	Rapid weighing	Ruscus aculifolius Viburnum tinus Laurus nobilis Arbutus unedo Olea europaea	1·22 5·53 4·26 6·20 12·80	1·01 1·1 0·72 2·22 3·39	... .	mg./sq.dm. min./ 2·26 2·20 1·26 2·91 4·24
Henrici (1940)	Pretoria, South Africa (large Karoo bushes) (summer rainfall area)	Rapid weighing	Olea verrucosa Rhus burchellii Rhus lancea Heteromorpha arborescens (mesomorph) Royenia microphylla (mesomorph)	... ...	....	Average over all Seasons { 5·33 4·33 3·16 8·16 7·83	mg./g./ min. 9·63 5·66
Poljokoff (1946)	Palestine (Maquis)	Rapid weighing	Ceratonia siliqua Olea europaea Prunus amygdalus (mesomorph)	....	....	4·95 4·07 13·37	8·72 10·22 29·89
Eckardt (1952)	Narbonnaise region (Garrigue)	Rapid weighing	Teucrium flurum Coronilla glauca Bupleurum fruticosum	12·0 20·4 9·0	1·1 2·0 1·0	....	. . .

* Transpiration rate is given as mg./sq.dm./min. for the *total area* of test leaves (*cf.* Rouschal, 1938).

The Rapidity of the Transpiration Stream

It is of interest to know whether there is any relationship between the rate of transpiration and the structure of the conducting elements. Huber (1932, 1937) pioneered research in this field and his methods were applied by Rouschal (1937-38) to the study of the rate of movement of the transpiration stream in Maquis plants with diffuse porous stem structure at Rovigno (see Table IV). In the moist season the average rate was 2.3 metres per hour (maximum rate 4.5 metres per hr.; minimum rate 1.5 metres per hr.), but in the late dry period it fell to 0.96 metres per hour (minimum 0.7 metres per hr.). In contrast the rates in ring, porous (mesomorphic) types ranged up to 45 metres per hour.

The stem structure of selected sclerophylls in Western Australia has been studied by the author who has found them also to be of the diffuse porous type. Preliminary work on rate of movement of the transpiration stream has given results rather higher than those obtained by Rouschal for Maquis sclerophylls under similar favourable conditions. It should be noted, however, that in studying Western Australian sclerophylls only the indigo-carmine and eosin dye method has been used and not the more accurate electrical conductivity method used by Rouschal. Values obtained by the dye method are known to be rather higher than those obtained by the electrical method, so that the rates for Western Australian sclerophylls must be considered as maximum values. The average rate for three test plants in late spring was of the order of 6.6 metres per hour and for the dry period in summer, 3.5 metres per hour.

TABLE IV

The Rapidity of the Transpiration Stream in Sclerophylls in Metres per hour

Rouschal (1938) at Rovigno (Mediterranean)			Grieve, Perth, Western Australia (hitherto unpublished data)		
Plant	Moist Conditions	Dry Conditions	Plant	Moist Conditions (late spring)	Dry Conditions (late Summer)
Arbutus unedo	1·5	0·7	Banksia attenuata	7·2	5·5
Laurus nobilis	3·1	1·2	Hibbertia hypericoides	6·6	1·5
Olea europaea	2·4	0·7	Stirlingia latifolia	6·9	3·4
Pistacia lentiscus	2·2				
Pistacia terebinthus	4·5	1·5			
Phillyrea media	2·0	0·7			
Average	2·3	0·96	Average	6·6	3·5

Both sets of results (Table IV) confirm Huber's prediction (1935) that rates would be relatively slow in diffuse porous sclerophylls with their numerous small vessels of greater conducting area as compared with ring porous types with their larger vessels but more restricted conducting area. It may be noted also that the sclerophylls of the eastern Mediterranean area and those of Western Australia show slower rates of dye movement in summer in agreement with the reduced transpiration rates described earlier.

The Osmotic Pressures of Sclerophylls

It now seems well recognised that sclerophylls as a group have a reasonably high osmotic pressure, particularly as compared with mesomorphs.

A summary of the data now available on the osmotic pressures of sclerophylls in Australia and in different parts of the world is presented in Table V. For typical sclerophylls in the Mt. Lofty Ranges in South Australia, Wood (1934) recorded by the plasmolytic method an average value of 22 atmospheres. For more arid areas (Koonamore) he found that the average osmotic pressure was considerably higher at 54 atmospheres. Grieve and McAleer using Barger's method with expressed sap, found an average of 20 atmospheres in late summer for sclerophylls near Perth, Western Australia. Values

for sclerophylls from the more arid areas in Western Australia are not yet available for comparison with those of arid South Australia. It may be noted, however, that under similar arid conditions in Arizona, Braun-Blanquet and Walter (1931) found an average of 30 atmospheres. For the Mediterranean area (including Corsica, the Northern Adriatic coast, Palestine and Algeria) average values ranging from 22-41 atmospheres have been reported (Table V).

It appears from these results that with one or two exceptions there is reasonable correspondence in the osmotic pressures of sclerophylls in different parts of the world. Most workers are in agreement also that a rise in osmotic pressure occurs in sclerophylls as one passes from the moist to the really dry period: Rouschal (1938) showed values of 21 atmospheres at Rovigno in early summer and of 37 in late summer; Grieve and McAleer working in the Perth area noted a marked rise in osmotic pressure of the sclerophylls, *Stirlingia latifolia, Hibbertia hypericoides, Bossiaea eriocarpa* and *Banksia menziesii* in passing from spring to summer. Braun-Blanquet and Walter (1931) by contrast however, reported no significant upward change in the osmotic pressures of plants in the Montpelier region on passing from winter to summer. This region, it may be noted however, is close to the northern limit of Mediterranean sclerophylls and may not be typical.

TABLE V

Osmotic Pressures of Sclerophylls

Australia

South Australia Wood (1934) (Plasmolytic Method)			Western Australia Grieve and McAleer (unpublished data) (Barger's Method)
(a) Koonamore (Arid) September (Spring)		(b) Mt. Lofty Ranges	Perth March (Late summer)
Acacia aneura .. .. 68 atm		*Eucalyptus odorata* .. .. 30 atm	*Banksia menziesii* . . 21 atm
Aracia burkittii . .. 55 ,,		*Acacia pycnantha* . . . 25 ,,	*Stirlingia latifolia* . 21 ,,
Eremophila scoparia .. .. 50 ,,		*Hibbertia stricta* . 21 ,,	*Hibbertia hypericoides* . . 27 ,,
Myoporum platycarpum .. 43 .,		*Xanthorrhoea semi-plana* . 15 ,,	*Bossiaea eriocarpa* . . 21 ,,
		Leptospermum myrsinoides . 18 ,,	*Hardenbergia comptoniana* 14 .,
			Kennedya prostrata .. .... 21 ,,

Mediterranean Area

	Braun-Blanquet & Walter (1931)	Oppenheimer (1932)	Killian & Faurel (1933)	Guttenberg & Buhr (1935)	Rouschal (1938)	Poliokoff (1949)	Konis (1949)	Eckardt (1952)
Arbutus unedo	24·0	....	....	33·2	40·6	....		
Arbutus andrachne	.	31·1		.	..	. ..	26·6	.
Capparis spinosa ..	...	....	21·3	. .	. ..			
Ceratonia siliqua	....	20·5	.	....		20·2	16·0	. .
Laurus nobilis ..	17·5	28·3		28·3	30·1		27·3	.
Nerium oleander	.		22·3				. .	.
Olea europaea ..	32·5	27·0	....	51·7	46·9	29·5		
Phillyrea media	.	....		60·2	49·5		40·0	
Pistacia lentiscus	24·0	....	.	28·4	29·0			
Pistacia palaestina	.	. ..	..		. .		21·7	
Quercus ilex ..	25·0	....	....	32·6	29·5			
Baplenrum fruticosum ..	...	....	....	.	.	..		40·0
Teucrium flavum	..	. .	....	....	. . .	....		37·5
Coronilla glauca ..	....		. .	.	.		.	42·5
Mesomorphs								
Reseda villosa	.		10·5	.		....		
Senecio coronopifolias		..	6·5	.		.		
Matthiola maroccana			8·0					
Moricandia suffruticosa			8·9			. ..		

Eckardt (1952), the most recent worker in this field has studied Garrigue vegetation in the French Mediterranean region, and found highly significant increases in osmotic pressures in plants with the passage from winter to summer conditions. During the wet season the average osmotic pressure of plants he tested was 13.7 atmospheres while during the dry season the average value rose to 40.7 atmospheres.

Compared with known results for mesomorphs (Maximov 1929; Killian and Faurel 1933) the values for sclerophylls are very much higher and the increasing dehydration of the protoplasm found in most instances with increasing dryness appears to be associated with decreasing transpiration rate. Boon-Long (1941) has made the suggestion that reduction in transpiration is brought about by the lowering of permeability of tissues to water consequent upon higher osmotic concentrations. Whether this is the case for sclerophylls still remains to be determined.

The Stomatal Frequencies of Sclerophylls

The question of stomatal frequency is important in relation to the effect of moist versus dry conditions on plants, but critical data is somewhat limited for sclerophylls in areas other than Australia.

Wood (1934) reported that for 39 different sclerophyll tree and shrub types in the Mt. Lofty area of South Australia, there was a stomatal frequency of 230 ± 19. The family Proteaceae was found to have a low stomatal frequency of 145 ± 19 while the Epacridaceae (302 ± 5) had a high one as did also the families Myrtaceae (301 ± 22) and Leguminosae (277 ± 21). Sclerophylls from the same families growing in more arid areas (Koonamore) were found to show no significant difference in stomatal frequency.

Wilson (1924) determined the stomatal frequencies of well watered pot grown seedling sclerophylls at Melbourne, Victoria. Analysis of his figures by Wood (1934) showed a mean frequency of 190 ± 15, which Wood considered did not differ significantly from his own results for the Mt. Lofty sclerophylls. Patton (1932) listed the number of stomata per sq. mm. in three legumes, *Platylobium obtusangulum* (280), *Bossiaea cinerea* (600), and *Acacia oxycedrus* (120), and of a Myrtaceous plant, *Leptospermum laevigatum* (100) occurring in heath sclerophyll vegetation at Cheltenham in Victoria and drew attention to the considerable degree of variation shown. This variation was also the subject of comment by Wood for South Australian plants. McLuckie and Petrie (1927) gave values

for some sclerophyll and rain forest plants of Mt. Wilson in New South Wales. While the data published is rather limited, it seems clear that for the plastic genus *Eucalyptus*, similar variation in stomatal frequency frequently occurs as was shown by Wood for South Australian Eucalypts. The mean value for the four New South Wales Eucalypts was 211 and for four members of the Proteaceae it was 154. This may be compared with the Mt. Lofty South Australian figures of 312 for five Eucalypts and 145 for eight members of the Proteaceae. The stomatal frequencies for the nine Mt. Wilson sclerophylls were high as compared with the four Rain Forest types (means 215 : 159 respectively) but from the data given it is not possible to say with certainty whether there is any significant difference. Carey (1938) has studied the stomatal frequency in a large number of sclerophylls from sandstone ridges around Sydney. For members of certain families she obtained a picture somewhat similar to that of Wood, e.g., for Proteaceae, the mean value was 162, for Epacridaceae 296, and for Leguminosae, 185.

Preliminary work on sclerophylls of the Swan coastal plain in Western Australia has shown a mean value of 270 for 18 species growing under conditions not markedly different from those of the Mt. Lofty Ranges in South Australia for which Wood recorded a value of 230 ± 19. Examination of stomatal frequency for individual families shows that there is considerable variation from those of South Australia and from those of the Sydney area, and further work is needed to extend the number of species for comparison purposes.

Detailed determinations on stomatal frequency in sclerophyll vegetation in the Mediterranean region appear to be lacking so that useful comparisons can not be made here.

Turning to the question as to whether high stomatal frequencies are associated with more xerophytic conditions as Salisbury (1927) suggested for Great Britain, Wood (1934) finds no support for this view. Statistical analysis showed that there was no significant difference between stomatal frequencies of South Australian sclerophylls and plants of British woodlands. Although a significant difference was found between stomatal numbers of South Australian sclerophylls and those of the dry patinas of Ceylon (Parkin and Pearson, 1904), Wood doubts the adequacy of Parkin and Pearson's data and concludes that generic and family characters are more important than environment in determining stomatal frequency. The stomatal index for South Australian sclerophylls was also found to be fairly constant (although relatively few species were tested) and to approximate to the mean value given by Salisbury for British woodland plants. Carey (1938) for sclerophylls in the Sydney area concluded that stomatal index was independent of environment. She could find no correlation, however, between stomatal indices of either family or genus. In view of these differences some further comparative investigation of stomatal frequency in sclerophylls from other arid and semi-arid parts of Australia, seems warranted.

Position of the Stomata

In most of the important families in which sclerophylls are represented in New South Wales, Victoria and in South and Western Australia, stomata may occur on both sides of the leaf. An exception is the Epacridaceae in which they are confined to the lower surface. Evenari (1937) in a study of desert plants (not sclerophylls) found more stomata on the upper than on the lower surface and suggested this might be due to the high light intensity. Wood's data (1934) is in direct contrast to this for South Australian arid region plants, for both tomentose succulents *(Kochia, Bassia)* and sclerophylls. Wood does, however, suggest that there may be an increase in the percentage of plants possessing stomata on *both* leaf surfaces when passing from temperate to arid conditions. Thus, in the Mt. Lofty area the percentage with stomata on both sides of the leaf is 79 while at the desert station of Koonamore it is 100.

Summary

The preceding analysis shows that sclerophylls as a class differ in their water relations from mesomorphs, particularly in the dry summer period. The average rate of field transpiration in mg./g./min. is lower than in mesomorphs as is also the rate of movement of the transpiration stream. On the other hand their osmotic pressures are higher than mesomorphs, and also rise with dry summer conditions. Stomatal frequencies and stomatal indices in sclerophylls appear, at least under Australian conditions, to show no correlation with habitat or environment, although there is a suggestion that the percentage of stomates on both surfaces of the leaf increases with increasing aridity.

The Assimilation and Respiration of Sclerophylls

Because of the summer drought conditions to which sclerophylls are normally exposed (due to climate or soil or both) it has been of considerable interest to ascertain whether they enter a period of enforced physiological rest at that time or whether the presence of the xeromorphic modifications they possess allows them to continue active photosynthesis. In the Mediterranean area careful studies have been made in particular of Maquis vegetation which provide answers to the above questions.

Guttenberg (1927) made a qualitative study of assimilation in Mediterranean sclerophylls under climatically favourable and unfavourable conditons. In spring (March-April), when the growth of new leaves was beginning, climatic conditions were very favourable, moisture being adequate and temperature mild, while the stomata were open at their maximum throughout the day, both in sun and shade. The osmotic pressure of leaves (by a plasmolytic method) was found to be approximately 36 atmospheres, while transpiration was relatively high and conditions were suitable for good assimilation. This was reflected by strong starch formation and storage in the leaves. The plants were next studied in summer (August) by which time a condition of extreme drought had de-

veloped. The stomata were found to be only silghtly open for a short time in the morning and for a considerably shorter time in the late afternoon while on many days they remained completely closed. The osmotic pressure was found to be much higher than in spring, ranging from 53-69 atmospheres. It was observed also that at the end of the summer period the leaves were more or less denuded of starch and low in sugar. This was taken as evidence that little assimilation occurred during the drought period. The tannin content was also observed to increase in the cells of leaves as the summer drought intensified. With the coming of the wet season the starch content was increased in the leaves for a period of some weeks, but it then began to fall again and by mid-winter had largely disappeared from the palisade cells.

Guttenberg and Buhr (1935) studied quantitatively the assimilation and respiration of Maquis in Corsica in spring and in summer. In spring assimilation was found to be high but in summer it was rather restricted. They concluded that under drought conditions the plants were on the threshold of survival and that a summer rest occurred. The almost complete stoppage of photosynthesis in summer was ascribed to relative lack of water.

Harder *et al.* (1931) worked on desert plants including the sclerophyll *Nerium oleander* (which is also one of the character plants of the Maquis). This shrub was found to occupy dried-out watercourses and even in summer (August) the subsoil remained moist and the stomata stayed open. In the early morning (7 a.m.-8 a.m.) assmilation was greater than respiration showing a positive balance of 3-5mg. CO_2/sq.dm./hr. at 30°C. By 10 o'clock, however, it had fallen to the compensation point where it remained until 4 p.m. after which time assimilation again rose above respiration. Shading of plants resulted in a rise of the rate of assimilation. These results are in general agreement with those of Guttenberg and Buhr. Harder *et al.* investigated respiration only in single cases where it was found to be 0.7 mg./sq.dm./hr. After rain, respiration was found to rise sharply, even under conditions of falling temperature. They believed this could be explained by re-hydration of the protoplasm. In contrast to the findings of Guttenberg (1927) and Guttenberg and Buhr (1935) for Maquis vegetation, Harder *et al.* found no evidence of a drought rest period in the desert plants they studied. Maquis of course has quite a long favourable seasonal period for growth, while desert plants have not and this may prove to be of importance in relation to the absence of a rest period. Killian (1933a) for *Pistacia lentiscus* in Algeria found an assimilation value of 10 mg./sq.dm./hr. in the spring. During summer (June) the curve sank between 11a.m. and 1 p.m. In the earlier part of the morning reasonable assimilation occurred but by the afternoon it was negligible. Eckardt (1952) reported for Garrigue (modified sclerophyll) plants that during the dry season photosynthesis practically stopped during the afternoon. He ascribed this to the interaction of a number of factors including relative lack of water, closure of stomata, protoplasmic reactions consequent upon dehydration of colloids and perhaps destruction or change in the chlorophyll pigments.

No quantitative work on photosynthesis or respiration has been done on Australian sclerophylls although Wood (1934) has followed the seasonal variation in carbohydrates. In the absence of experimental work it is not possible to say with certainty whether Australian sclerophylls show greatly reduced assimilation during the dry summer period. Diels (1906) has described vividly the appearance of the dried-out looking vegetation in Western Australia in late summer and suggested that the plants pass largely into a state of suspended animation. It is a matter of common observation that Western Australian species such as *Hibbertia hypericoides*, *Stirlingia latifolia*, *Bossiaea eriocarpa* and *Acacia acuminata* show with increasing dryness a marked yellowing of photosynthetic tissues. Normal green colour returns very rapidly if shoots from these plants are placed in water. The same effect is observed in intact plants after the commencement of the winter rains. It therefore seems possible that photosynthesis may be affected particularly during the latter period of the summer. Studies are now proceeding on Western Australian sclerophylls under field conditions to obtain the necessary quantitative data to clarify this point.

The Metabolism of Sclerophylls

Study of the metabolism of sclerophylls in the Mediterranean region and in semi-arid and temperate Australia has shown some interesting features. Guttenberg (1927) examined starch-sugar-tannin relationships on a qualitative basis in Maquis. He showed that in the spring, starch content was high, the cells of leaves being packed with starch grains. Passing into summer the starch disappeared, and sugar concentration decreased, indicating rapid further breakdown or alteration of products of starch hydrolysis. During this period of increasing drought the tannin content of leaf cells was observed to increase. With the onset of first winter rains, starch grains reappeared but later in deep winter a second reduction in starch content occurred. No determinations appear to have been made to see whether there was any change in sugar content at that time. Wood (1933) in South Australia followed the seasonal variations in carbohydrate content in a broad sclerophyll plant (*Acacia pycnantha*) and in a needle-leaf sclerophyll (*Hakea ulicina*). Sugar concentrations were found to rise during periods of low temperature and vice versa. The starch concentration was found to be greatest when sugar concentration was low and high sugar was correlated with the period of active growth in each sclerophyll type. This led him to the view that high sugar concentration was related to cellulose wall formation. He noted that there was no difference in sugar/starch relations from other plants or in their seasonal variation.

Wood (1933) seems to have been the only worker so far who has concerned himself with the processes of lignification, cutinization and the changes in tannin content in sclerophylls. Study of these processes is of particular interest under southern Australian conditions where these features are highly developed in sclero-phylls. Wood observed that the process of lignification started in broad sclerophyll (*Acacia pycnantha*) leaves only when they were reaching maturity after some two months growth (see Table VI) and that lignification proceeded from the base towards the tip of the leaf.

TABLE VI

Process of Lignification in Southern Australian Sclerophylls (after Wood 1933)

		Broad Sclerophyll *Acacia pycnantha*			Needle-leaved Sclerophyll *Hakea ulicina*				
		Young	Developing	Mature	2 weeks	6 weeks (Mature)	6 months	18 months	30 months
Lignin (%)	....	0·97	3·2	3·2-3·4	0·65	4·84	5·4	5·5	6·6
Cutin (%)	....	0·4	5·8	7·6-8·2	2·0	9·3	13·8	13·9	13·8
Tann'n (%)	....				10·4	8·6	6·0	5·6	....

For needle-leaved sclerophylls, e.g., *Hakea ulicina* which mature in one month but stay functional for three years, there was a continuous increase of lignin with time up to 30 months (see Table VI). As was the case in *Acacia*, the lignification also proceeded upwards from the base of the leaf. The process of cutinisation seemed to be completed by the time the leaf was six months old. Tannin concentration fell with time, and Wood showed that there was a relation here with lignification. Tannin (a product intimately connected with sugar metabolism) is believed to be concerned through its phenolic nucleus with the formation of the lignone complex of lignin. As the presence of thick cellulose walls impregnated with lignin and cutin is such a feature of Australian sclerophylls this is one of the aspects of sclerophylly which requires further study in different parts of the Commonwealth.

The Significance of the Xeromorphic Modifications Found in Sclerophylls

Sclerophylls as a Type of Xerophyte

Any discussion on the significance of xero-morphy in sclerophylls involves consideration of the larger question of xerophytes. In its original sense this word referred to plants which grew in dry areas of the world (Schouw, 1822). Schimper (1903) and Warming (1909) introduced as well physiological and morphological concepts so that a xerophyte came to be regarded as a plant which was exposed to conditions of deficient water supply or which grew in dry places and with which certain morphological features were associated. Maximov (1929) introduced a different physiological concept for xerophytes, characterising them as plants with a high resistance to desiccation. Under both conceptions xerophytes included a variety of plant types:—succulents, perennial semi-succulents, tomentose succulents (saltbushes), non-succulent perennials (herbaceous xerophytes), plants which shed their leaves under very dry conditions, and sclerophylls. It is in this last group, with which we are essentially concerned, that the majority of the morphological modi-

fications described as xeromorphic characters occur. Sclerophylls were defined by Schimper (1903) as plants of the xerophytic bush in sub-tropical regions, where the rain falls in winter. Maximov (1929) enlarged the habitat to include arid regions. As we have seen earlier the main areas of occurrence of sclerophyll vegetation are in the Mediterranean regions, California, Central Chile, the Cape Province of South Africa, and South and Western Australia. It is of considerable interest at this point to examine further the occurrence and distribution of the sclerophyll habit under Australian conditions to see how far it conforms to the above definition of habitat and whether all of it is necessarily xerophytic.

Wood (1924) stated that sclerophylls with their characteristic xeromorphic modification occurred not only in the arid regions of South Australia, but also wherever evaporation was markedly in excess of rainfall as in the sclerophyll forests of the Mt. Lofty Ranges near Adelaide where the rainfall range was from 20 to 40 inches. Osborne (1932) pointed out that for Sydney, near which on the Hawkesbury Sandstone there is a strong development of sclerophyll vegetation, the annual rainfall is 48.2 inches with a mean fall of 2.6 inches during the driest month. The average annual evaporation is 38.45 inches and it exceeds rainfall only during four summer months. The Transeau Ratio (P/E) is approximately 1.3. According to Osborne the Sydney ratio is thus comparable with that of United States cities such as Boston (Mass.), and New Orleans (La.) which come within the area of "southern mesophytic forest" (Livingstone and Shreve, 1921) and yet it has a well developed sclerophyll vegetation. Osborne observed, however, that the plants of the Hawkesbury Sandstone did suffer from periodic drought due to the drying out in summer of the shallow sandy soil in better drained areas. Patton (1932) in discussing the extensive evergreen sclerophyllous vegetation of the sand heaths east of Port Philip Bay in Victoria, stated that while the six summer months from October to March actually received slightly more rain than the six winter months, nevertheless the evaporation during the six summer

months greatly exceeded precipitation. As in the Sydney area the soil factor here is regarded as being more important than climate because of the inability of the soil to retain much water. After a prolonged period of drought, Patton records that the water content of the soil at a depth of 12 inches fell as low as 1.07 per cent.

For the area around Perth where typical sclerophyll vegetation occurs, the average annual rainfall is 34.7 inches and the average annual evaporation is 34.5 inches. The rain falls in winter and for the six summer months of the year evaporation is high and very dry conditions prevail. Passing south towards Albany the climatic conditions approximate more closely to those of Sydney. The vegetation remains markedly sclerophyll in character (becoming modified, however, in the Karri forest) and the country is subject to summer drought. Passing inland the environment rapidly becomes more arid and the degree of sclerophylly more marked. The soil factor is again of great importance because the sandy soils tend to become very dry in summer.

Under all the Australian sclerophyll habitats so far mentioned summer drought is always a possibility and the soils are such that they dry out quickly. Certain areas conform exactly to the picture of Mediterranean climate and other areas fit reasonably with Schimper's conception of habitat of sclerophylls because the *effective* rain is mainly in the winter months (*cf.* Patton 1932, page 209). Sclerophylls growing in these areas although always xeromorphic may not necessarily be xerophytic. This has to be determined by experiment.

Not all the sclerophyll vegetation in Australia, however, is confined to the winter rainfall area. On the mainland it extends through New South Wales up to Queensland where the rainfall shows a marked summer maximum and may exceed evaporation during each month of the year. Sclerophylls in this area under our present climate could not come into the category of xerophytes. The same applies to those in Tasmania where Rodway (1914) observed that although the climate of Tasmania was distinctly temperate the larger plants were of decidedly xerophytic (sclerophyll) nature.

This matter will be referred to again when dealing with the origin of sclerophylly.

The Rate of Water Loss from Xerophytic Sclerophylls

Schimper (1903), Benecke-Jost (1924) and others popularized the view that xerophytes, which grew in dry places where water was the most limiting factor, transpired at a lower rate than soft leaved plants in temperate habitats.

Little experimental evidence existed for Schimper's assumption that they did transpire at a low rate but Schimper so profoundly influenced thought at the time that it was many years before his view was seriously questioned. In 1916 the experimental gap first began to be filled when Maximov showed that xerophytic plants in the semi-desert area at Tiflis in Russia transpired at a higher rate than soft leaved plants from a shaded irrigated garden. Further papers by Maximov, Alexandrov (1922), Huber (1924), and Stocker (1928), appeared to confirm the view that xerophytes as a class transpired faster than mesophytes. In his book, "The Plant in Relation to Water" (1929), Maximov strongly advocated this view and appeared to make exceptions only of the succulents of the cactus type and those plants with continually blocked or deeply sunken stomata. Maquis sclerophylls were considered as belonging to the group which transpired faster than mesophytes under favourable conditions. It is worth noting that none of the xerophytes studied by Maximov near Tiflis or those investigated by other Russian workers such as Vasiliev (1931) appear to be of the sclerophyll type. Seybold (1929) using evergreen plants including at least one typical Maquis plant (*Laurus nobilis*) demonstrated that their transpiration was below that of mesophytic plants and criticized the general conclusions of Maximov. Maximov (1931) replied that these evergreens were not true xerophytes and reiterated his view that true xerophytes of desert regions had a higher transpiration rate than mesophytes. Maximov (1929, 1931) therefore substituted "drought resistance" for the transpiration criterion. Xerophytes were to be distinguished not by reduced transpiration but by the capacity to survive drought and dehydration of tissues with little or no injury. The revised Schimper definition according to Maximov (1931) should read:—"Xerophytes are plants of dry habitats which are able to decrease the transpiration rate to a minimum when under conditions of water deficiency". So far as can be ascertained, however, Maximov has given no experimental evidence on the march of transpiration of a xerophyte when passing from moist season to drought, to indicate when the reduction of transpiration would occur. Moreover it almost appears that sclerophylls are excluded from his concept of "true xerophytes", since they are not restricted by any means to desert areas. With the passage of years, intensive work on transpiration, particularly in areas subject to summer drought has led to accumulation of a considerable body of data, the relevant parts of which in the case of sclerophylls have been reviewed earlier in this paper. Some disagreement with Maximov's viewpoint has emerged.

Henrici in South Africa (1937, 1940a, 1940b) pointed out that the Karroo types of xerophyte (including large Karroo sclerophylls) were different from Maximov's Tiflis type, because only rarely did they transpire highly even in the presence of adequate water. They not only restricted their water loss with declining water supply of the soil, but also restricted transpiration even with adequate water during the hot part of the day. She indicated that Maximov's (1929) findings on the "high transpiration of xerophytes" applied for Karroo bushes only when the soil was about half saturated, a condition which was seldom met with on the veld. While she agreed that (under specific conditons) plants in drier regions undoubtedly had the ability to transpire freely, it was more important to know what the plants did under the adverse conditions which probably prevailed for a great part of their lifetime.

41

Oppenheimer (1951) in reviewing work on water relations of plants in the Middle East, claimed that xerophytes with xeromorphic structures had a lower average transpiration rate than mesomorphs provided that total average water use was expressed in terms of fresh weight of plant or per unit of soil area permeated by the roots. While agreeing that Maximov was probably right in demonstrating that certain xerophytes have very high transpiration intensities when well supplied with soil moisture, he differed from that author in contending that xerophytes (including sclerophylls) lived normally under conditions of low water supply during the summer in the Middle East and did reduce their water loss before a condition of extreme water deficiency supervened. This view is essentially similar to that of Henrici. Oppenheimer claimed further that even if the transpiration rate of xerophytes did at times exceed that of a mesophyte the overall loss was still less because of greatly reduced leaf area. Here he opposes the views of Stocker (1923) and of Thoday (1931) that the reduction in size of the sclerophyll leaf has been accompanied by a more than compensating increase in the total leaf area because of the total number of leaves present. In this connection Patton (1932) had earlier criticized Thoday's view, as his study of Victoria heath sclerophyll vegetation had provided evidence to show that the total leaf area did not compensate for the generally small size of the leaves. The author's observations on Victorian and Western Australian sclerophylls, support the contentions of Oppenheimer and of Patton.

Patton (1932) also held that the sclerophyllous heath vegetation of the Cheltenham area in Victoria needed to economise water during the regularly recurring drought period. He did not cite any transpiration experiments but stated that the restriction of transpiration was accomplished not only by the reduced size of leaves, but also by the reduction of total leaf area.

Wood (1933, 1934, 1939) believed that his transpiration results for Australian sclerophylls, taken together with results of overseas workers on xerophytes, mesophytes and shade plants in Swedish Lapland, Germany, the Tyrol, the Mediterranean region and Arizona, disposed equally of the older view that xerophytes had a reduced transpiration rate compared with other plants and of Maximov's contention that they had an increased one. Plants from the diverse habitats mentioned were stated to have a mean transpiration per unit area of 1500-2000 mg./sq.dm./hr. (25-33 mg./sq.dm./min.) A study of his results (see Table II) would not appear to bear out this statement for South Australian sclerophylls. Thus his average value for the Dilkera, Curnamona, Koonamore and Mt. Lofty areas is 5.4 mg./sq.dm./min. The average rate for the Dilkera and Curnamona areas is 1.8 mg./sq.dm./min. Only in the Mt. Lofty area is the average rate somewhat high (16.94 mg./sq.dm./min. with a range from 7.0-26.6 mg/sq.dm./min. As mentioned earlier these results are well above those obtained by the author for similar sclerophylls in comparable areas in Victoria and Western Australia under field conditions in summer. In any case even the Mt.

Lofty results scarcely come within the range Wood mentions for other areas. Study of the results of workers elsewhere on sclerophylls (see Table III) show their figures to be well below the 25-33 mg./sq.dm./min. Only in the case of mesophytic plants growing under comparable conditions (including Wood's own result for the mesomorph *Seneeio magnificus* at Curnamona) are there clearly indicated higher rates of transpiration. It may be noted that the rate for *Senecio magnificus* approximates very closely to that given by Maximov (1929) for mesophytic sun plants such as *Erodium ciconium* and *Hirschfeldia adpressa* at Tiflis. It therefore appears to the author that southern Australian sclerophylls, growing in areas subject to summer drought (due to either climate or soil or both) have *as a class* lower average rates of transpiration than mesomorphs growing under comparable conditions in summer and that they reduce their water loss before extreme water deficiency conditions develop. The different physiological groupings within the sclerophyll class under Southern Australian conditions will not be considered here, nor the sclerophyll types which, as has been mentioned, grow in areas in Australia where the climatic and soil conditions indicate that they are not xerophytes.

The Function of Xeromorphic Modifications in Sclerophylls

Schimper (1903) believed that the function of xeromorphic characters was to reduce water loss. Maximov (1929, 1931) when he found that the water loss of xerophytes with xeromorphic modifications (growing in Tiflis) was greater than that of mesophytes there, concluded that these structures were only of protective value when the plant was wilting. Bennett-Clark (1945) accepted Maximov's conclusion that the function of xeromorphic modifications was not to hinder water loss. As their occurrence seemed to him scarcely accidental, however, he suggested that they might serve to facilitate photosynthesis acting as mechanisms which protected the stomata and enabled them to keep open longer during drought conditions. Thus they would actually favour increase of transpiration, and of course, the diffusion capacity of the epidermis for carbon dioxide. He suggested that they operated by maintaining a relatively moister atmosphere around the stomata and neighbouring epidermal and mesophyll cells than would otherwise be found, thus inhibiting closure and maintaining high diffusion capacity. Bennett-Clark argued from this that leaves deprived of say, hairy coverings, should have less widely open stomata and so should transpire less. He tested this experimentally but while there was some suggestion of reduction in shaved leaves under very dry conditions he could not show the results to be significantly different from water loss of unshaved leaves. In other experiments using leaves of rolled plants which had been forcibly unrolled, Bennett-Clark found no significant difference between their transpiration rates when both were exposed to an atmosphere of about 40 per cent. relative humidity. If leaf

inrolling had physiological significance in the Schimper sense the transpiration in the rolled leaves should have been lower. Bennett-Clark suggested as explanation that the stomata were protected or prevented from shutting by being enclosed in the rolled leaf. These experiments were done under laboratory conditions and would need testing under field conditions. It may be noted, however, that there are already available certain results for sclerophylls and also tomentose succulents (saltbushes) which bear somewhat unfavourably on the theory. Thus Guttenberg and Buhr (1934) have shown in the case of Maquis that considerable reduction in rate of photosynthesis occurs with advancing summer and that plants enter upon a resting period. Eckardt (1952) has also shown for Garrigue vegetation that both photosynthesis and transpiration decrease during the dry season and that depression of transpiration in the afternoon may occur independently of any change in photosynthetic activity. Wood (1923, 1932), has also demonstrated very effectively for South Australian tomentose succulents (saltbushes) growing in semi-arid areas, that as compared with mesophytes, there is a strikingly low transpiration rate and also a lower photosynthetic rate. In the light of these results for two types of xeromorphs and also of other data presented on control of transpiration in sclerophylls it seems somewhat unlikely they function in the manner Bennett-Clark suggested.

Oppenheimer (1951) in discussing the structural peculiarities of sclerophyllous evergreens indicated that the studies of such early workers as Guttenberg (1907) suggested that thick epidermal walls, cutinization and sunken stomata were effective means of protection against water loss in times of emergency. Having noted that later authors felt unable to corroborate these conclusions by experimental studies, he went on to emphasize that his experience with plants growing under natural conditions in Palestine led him to support the classical interpretation. He instanced some of his work (1947) on sclerophyllous species of the Maquis where a considerable transpiration was suddenly reduced to zero by stomatal regulation. As he pointed out this can only be understood by the assumption that cuticular transpiration was not taking place or was negligible and that stomatal regulation was highly effective.

Henrici (1940a) examined the question of stomatal opening in relation to transpiration of large sclerophyllous bushes of the Karroo. For these plants the low daily water losses in times of drought was found to be due to stomatal control. The stomata either remained closed all day or they closed after a short period of rapid transpiration, so that transpiration values scarcely exceeded those of cuticular transpiration for the whole day.

From studies on Western Australian sclerophylls the author has concluded that stomatal regulation plays a large part in controlling water loss, although other internally operating factors (osmotic and protoplasmic) are believed to be concerned.

The evidence for control of water loss from sclerophylls in the three areas mentioned seems to point to some differences from the views of Maximov (1931) for xeromorphic xerophytes. Giving a hypothetical case of a xerophyte exposed to increasing dryness, Maximov states that "when the plant is wilting, when its stomata are closed and when the loss of water takes place only through the cuticle, then all these anatomical peculiarities manifest their protecting properties".

The experimental evidence for sclerophylls (and also for several other non-sclerophyllous xerophytes (cf. Henrici, 1940b; Oppenheimer 1951) is that average water loss is lower and that stomatal control (with the assistance of the xeromorphic features) may occur long before the plant is at the wilting stage.

Theories of Origin of Xeromorphic Modifications

Turgor Theory and the Experimental Induction of Xeromorphy (Xeroplasty)

Kohl (1886) believed that the development of "protective means" as the modifications were then described, was due to strong transpiration. He based this on the experimental induction of xeromorphic features (such as thick cuticle, thickening of epidermal walls, etc.) in plants growing in dry air. Schimper (1903) by contrast concluded that it was the amount of transpiration relative to water supply, rather than the absolute transpiration which was responsible. Zalenski (1904) confirmed Kohl's observations noting that leaves of plants growing in dry open habitats were more xeromorphic than those of plants growing in woodland shade. Rippel (1919), Alexandrov (1922), Tumanov (1927), Maximov (1916, 1929), and others confirmed experimentally that some xeromorphic characters could be induced by growing plants under dry conditions. Maximov (1929) stated that the xeromorphic modifications in the xerophytes he worked with were induced by solar radiation and water deficit in the leaves. Normal development of cells was considered to be prevented owing to lack of water in the embryonic tissues and consequently cells remained smaller and developed thicker walls. Other structural peculiarities followed from this.

Walter (1926) explained on a basis of osmotic pressure effects how reduced turgor would result in decreased size of cells and the development of more numerous stomata. Ashby (1933) produced supporting evidence by showing that increase of xeromorphy was correlated with reduced turgor in upper leaves.

It was pointed out by Thoday (1933), that as some plants (in particular many xerophytes) were relatively non-plastic and their xeromorphic features were hereditary, that Maximov's use of the term "xeromorphic" in relation to the above was confusing. Thoday therefore suggested "xeroplastic" as a more appropriate word to cover those conditons where features of form and structure suggestive of xerophytes or xeromorphy, could be shown by experiment to be produced or intensified by desiccating conditions. He stated that similar features shown

by a desert plant or sclerophyll plant in less arid areas, could not be assumed to be xeroplastic until experiments with that species had demonstrated them to be so. Daubenmire (1947) supported this view indicating that xeroplastic features were induced by drought and so only occurred under dry conditions, but because of genetic fixity xeromorphic features were inherited under any environmental conditions. According to Thoday (1931) the development of the microphyllous sclerophyll habit (ericoid, pinoid leaves) may be related to reduction of internal resistance so that no part of the mesophyll is more than a short distance from the main channels of supply. The experimental evidence suggesting this was first put forward by Yapp (1912). Martin (1943) has also pointed out that the smallness of the leaf blade renders it less likely to over-heat under semi-arid or arid conditions.

Xeromorphy due to Altered Metabolic Flux due to Mutations in Protoplasmic Constitution

Wood (1933) very aptly pointed out that the work on induced xeromorphy described above was developed in relation to upper and lower leaves of annual or mesophytic plants and by an *ad hoc* argument transferred to xeromorphs generally. For southern Australian plants growing in sclerophyll forests he considered that Maximov's theory of origin of xeromorphic characters could not apply, as leaves of such plants were not subjected to high tension of meteorological factors. Growth according to Wood "commences early and the foliar organs attain mature size and structure in the great majority of cases during the wet winter months. During these months the ground in the sclerophyll forests is saturated with water, the rainfall exceeds the evaporation to a considerable degree, the mean relative humidity is high and the mean temperature low." He could find no lack of turgor in cells of typical sclerophylls, e.g., *Hakea ulicina* and *Acacia pycnantha*, during the period of development, such as Yapp (1929) found in *Spiraea*. Wood further pointed out, as we have noted earlier, that the sclerophyll type of vegetation is not confined to the Southern regions with a Mediterranean climate, but occurs also in eastern New South Wales and Queensland, where the rainfall shows a summer maximum and where rainfall exceeds evaporation during each month of the year. He therefor concluded that the outstanding characteristics of Australian xeromorphic (sclerophyll) plants were not determined by water deficits. From biochemical studies of sclerophylls he concluded that they were, however, determined by fundamental changes in the metabolic flux of carbohydrates. These changes he believed were probably due to a deep-seated mutation of protoplasmic constitution.

While agreeing that lignification and cutinization characteristic of sclerophylls may proceed from an altered metabolic flux, the author nevertheless is of the opinion that the generalization made regarding the absence of water deficits in Australian sclerophylls is rather too sweeping.

Although detailed information is still lacking there is reason to believe that in many sclerophylls, embryonic leaves are developing at a time of water stress and this as Nordhausen (1903) (cf. Maximov (Yapp) 1929) has indicated may pre-determine stomatal size and number, thickness of walls etc. A study of leaf ontogeny therefore seems necessary before it can be stated categorically for all existing Australian sclerophyll vegetation that the water factor is not concerned in the development of the xeromorphic modifications characterizing sclerophylls. The habitat of many Western Australian sclerophylls, the conditions obtaining during their vegetative growth phase and the transpiration results in summer drought also suggest that climatic stress must still be considered in relation to the origin of xeromorphy.

Xeromorphy due to mineral nutrition

In the course of work on nitrogen nutrition in plants, Mothes (1932) discovered that it was possible to induce certain xeromorphic features in plants by nitrogen deficiency. He considered that low nitrogen like a water deficit, induced high osmotic pressures which in turn brought about xeromorphic features. Marthaler (1939) continued this line of investigation and concluded from his studies of high moor plants in Germany, that nitrogen had no specific effect in relation to xeromorphy, although relative lack of the element did induce some xeromorphic characters. Wood (1934) put forward the view that the deficiency in mineral bases other than alumina and iron in the areas where Australian sclerophyll vegetation grows, might be responsible for their xeromorphy. Beadle (1953) compared the development of plants on the relatively fertile Wianamatta Shales and Narrabeen Shales (which are rich in phosphate) with the stunted, highly xeromorphic sclerophyll vegetation characteristic of the Triassic Hawkesbury Sandstone. Pot culture experiments with fertilizers suggested to him that the degree of xeromorphy of the leaves of some plants was determined by the supply of both phosphate and nitrate.

Specht (1952) working in South Australia on the sclerophyll vegetation of the light land area of the ninety mile plain has taken a more conservative view as to the influence of nutrients in relation to xeromorphy.

From the evidence so far to hand it seems that the effect of lacks in mineral nutrition in inducing xeromorphy must be regarded as a valuable line of enquiry, but it appears necessary to determine whether we are here dealing with a xeroplastic effect or really getting at the origin of xeromorphy. It seems likely that more progress in determining this might be made by the comparison of selected sclerophylls grown from seed in manured and non-manured plots under natural conditions. So far it should be noted that the more striking xeromorphic features of sclerophylls, namely sunken stomata and pits and great development of cuticle and woody tissue (lignification) have not been produced or suppressed by experimental treatments.

Xeromorphy due to intense light

It has been shown by many workers (Bergen 1904, Penfound 1931, Turrell 1944, Shields 1951) that intense light can induce a certain degree of xeromorphy in plants. The criteria used in assessing this increased xeromorphy were greater thickness of leaf and of palisade tissue. As in the case of mineral nutrition the criticism may be made here that the effects produced are possibly only of a xeroplastic nature. No experimental evidence on the formative effect of light under field conditions appears so far to be available for sclerophylls and firm conclusions must await new experiments in this direction.

Summarised Conclusions

The examination of the physiology of sclerophylls growing in areas of summer drought has shown that as a class they possess certain well defined features which mark them off from some other xerophytes, and from mesophytes. In their water relations they show a capacity to restrict transpiration during the summer so that on the average they lose water at a lower rate than mesophytes and xerophytes of the type studied by Maximov. Restriction of transpiration is achieved partly by stomatal closure (when the characteristic xeromorphic modifications can exercise their effect), partly by the opera-

tion of a protoplasmic factor arising out of altered osmotic pressure which increases with advancing summer, and partly by reduction in overall leaf area particularly in ericoid and needle-leaf sclerophylls. In contrast to the types of xerophyte studied by Maximov the restriction of transpiration in Karroo sclerophylls, Maquis and Australian types of sclerophyll may occur well before conditions of extreme water deficiency supervene. Photosynthesis also shows progressive reduction with advancing dry season and in contrast to some semi-desert xerophytes, Maquis sclerophylls appear to pass into a period of greatly reduced physiological activity. Their metabolism shows many points of difference from that of other plants, the emphasis in the broad leaf and needle leaf types being upon lignification and cutinisation which takes place when the leaf is reaching maturity. The xeromorphic modifications stem from the above alterations in metabolism, but their origin remains obscure. Modifications so far induced experimentally appear to be xeroplastic in nature and further research is required to determine to what extent inadequate supplies of water, lack of essential elements at significant phases of growth, or high solar radiation, condition true xeromorphy in sclerophylls.

References

Ashby, E., 1933. *Sch. Sci. Rev.* 55: 329.
Adamson, R. S. & Osborne, T. G. 1924. *Trans. roy. Soc. S. Aust.* 48: 87.
Alexandrov, W. 1922. *Monit. Jard. bot Tiflis.* Ser. II, livr., 1, 57. (Russian with French abstract).
Beadle, N., 1953. *Ecology* 34: 426.
Benecke-Jost. 1924. "Pflanzenphysiologie." 4th Edition. Jena.
Bennett-Clark, T. 1945. *J. R. Coll. Sci.* 15: 99.
Bergen, J. Y. 1904. *Bot. Gaz.* 38: 285.
Boon-Long, T. 1941. *Amer. J. Bot.* 28: 333.
Braun-Blanquet, J. & Walter, H. 1931. *Jb. wiss. Bot.* 74: 697.
Carey, G. 1938. *Proc. Linn. Soc. N.S.W.* 63: 439.
Cooper, W. 1922. Carnegie Inst Wash. No. 319.
Daubenmire, R. 1947. "Plants and Environment". (Wiley & Sons: New York.)
Diels, L. 1906. "Die Pflanzenwelt von West Australien". Die Vegetation der Erde. VII. (Engelmann: Leipzig.)
Diels, L. & Pritzel, E. 1905 "Fragmenta Phytographiae Australiae occidentalis". (Engelmann: Leipzig.)
Eckardt, F. 1952. *Physiol. Plant.* 5: 52.
Evenari, M. & Richter, R. 1937. *J. Linn. Soc. (Bot.)* 51: 333.
Firbas, F. 1931. *Jb. wiss. Bot.* 74: 459.
Guttenberg, H. Von. 1907. *Englers bot. Jb.* 38 (4-5): 383.
Guttenberg, H. Von. 1927. *Planta* 4: 726.
Guttenberg, H. Von., & Buhr, H. 1935. *Planta* 24: 163.
Harder, R., Filzer, P., & Lorenz, A. 1931. *Jb. wiss. Bot.* 75: 45.
Henrici, M. 1937. *Sth. Afr. Jour. Sci.* 34: 61.
Henrici, M. 1940a. *Sth. Afr. Jour. Sci.* 37: 156.
Henrici, M. 1940b. *Sci. Bull.* 185. (Govt.-Printer: Pretoria.)
Huber, B. 1932. *Ber. dtsch. bot. Ges.* 50: 89.
Huber, B. 1935. *Ber. dtsch. bot. Ges.* 53: 711.
Huber & Schmidt, E. 1937. *Ben. dtsch. bot. Ges.* 55: 514.
Killian, Ch. 1932. *Bull. Soc. bot. Fr.* 79: 185, 460.
Killian, Ch. 1933. *C. r. Acad. Sci. Paris* 196: 804.
Killian, Ch. & Faurel, L 1933. *Bull. Soc. bot. Fr.* 80: 775.
Kohl, E. 1886. "Die Transpiration der Pflanzen". Braunschweig.
Konis, E. 1949. *Ecology.* 30: 425.
Livingstone, E. B. & Shreve, F. 1921. Carnegie Inst. No. 284
Marthaler, H. 1939. *Jb. wiss. Bot.* 88: 723.
Martin, E. 1943. Carnegie Inst. Publ. No. 550.
Maximov, N. A. 1916. *Jour. Soc. Bot. Russ.* 1: 56.
Maximov, N. A. 1929. "The Plant in Relation to Water". (Allen & Unwin: London.)
Maximov, N. A. 1931. *J. Ecol.* 19: 273.
McLuckie, J. & Petrie, A. 1927. *Proc. Linn. Soc. N.S.W.* 52: 161.

Montemartini, L. 1930. *Inst. Bot. Palermo.* 1: 183.
Mothes, K. 1932. *Biol. Zbl.* 52: 193.
Nordhausen, M. 1903. *Ber. dtsch. bot. Ges.* 21: 27.
Oppenheimer, H. 1932. *Ber. dtsch. bot. Ges.* 50a: 185.
Oppenheimer, H. 1947. *Palest. Jr. Bot. Reh. Ser.* 6: 63.
Oppenheimer, H. 1951. *J. Ecol.* 39: 356.
Osborne, T. G. 1932. *Proc. Linn. Soc. N.S.W.* 57: VI.
Parkin, J. & Pearson, H. 1904. *J. Linn. Soc. (Bot.)* 35: 430.
Patton, R. T. 1933. *Proc. roy. Soc. Vict.* 45 (N.S.) Pt. II: 205
Penfound, W. T. 1931. *Amer. J. Bot.* 18: 558.
Poljokoff, A. 1945. *Palest. J. Bot. Jerusalem* Ser. 3, 138.
Rippel, A. 1919. *Beih. bot. Zbl.* 36: 187.
Rodway, L. 1914. Tasmanian Handbook B.A.A.S. 96, Hobart.
Rouschal, E. 1937. *S. B. Akad. Wiss. Wien.* Kl. Abt. 1, 146: 119.
Rouschal, E. 1938. *Jb. wiss. Bot.* 87: 436.
Salisbury, E. J. 1927. *Phil. Trans. Ser. B.* 216: 1.
Schimper, A. F. W. 1898. "Pflanzengeographie auf physiologischen Grundlage". Jena. (English Translation. Clarendon Press: Oxford, 1903.)
Schouw, J. F. 1822. "Grundtraek til en almindelig plantengeografie." Kobenhavn.
Schratz, E. 1931. *Jb. wiss. Bot.* 74: 153.
Seybold, A. 1929. Gesamt. gebiet der Bot. herausg. v. Gobel. Berlin II.
Shields, L. 1951. *Amer. J. Bot.* 38: 175.
Specht, R. L. 1952. A.N.Z.A.A.S. Sydney Meeting.
Stocker, O. 1923. *Z. Bot.* 15: 1.
Stocker, O. 1928. "Die Wasserhaushalt aegyptische Wusten und Salzpflanzen". Jena.
Thoday, D. 1931. *J. Ecol.* 19: 297.
Thoday, D. 1933. *J. Ecol.* 21: 1.
Tumanov, J. 1927. *Planta* 3: 391.
Turrell, F. M. 1944. *Bot. Gaz.* 105: 413.
Vasiliev, J. 1931. *Planta* 14: 225.
Walter, H. 1926. "Die Anpassungen der Pflanzen an Wassermangel". München.
Warming, E. 1909. "Oecology of Plants". (Clarendon Press: Oxford.)
Wilson, H. W. 1924. *Proc. roy. Soc. Vict.* N.S. 36: 175.
Wood, J. G. 1923. *Trans. roy. Soc. S. Aust.* 47: 259.
Wood, J. G. 1924. *Trans. roy. Soc. S. Aust.* 48: 226.
Wood, J. G. 1932. *Aust. J. Exp. Biol. Med. Sci.* 10: 89.
Wood, J. G. 1933 *Aust. J. Exp. Biol. Med. Sci.* 11: 139.
Wood, J. G. 1934. *J. Ecol.* 22: No. 1. 69.
Wood, J. G. 1939. A.N.Z.A.A.S. Presidential Address, Section M.
Yapp, R. H. 1912. *Ann. Bot.* 26: 815.
Yapp, R. H. 1929. See Maximov (1929).
Zalenski, V. 1904. *Mem. Polytech. Inst. Kiev* 4: 1 (In Russian).
Zalenski, V. 1923. *Bull. Univ. Saratov* 1-4 (In Russian).